RESEARCH ARTICLE

Range expansion drives the evolution of alternate reproductive strategies in invasive fire ants

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Abstract

Many species are expanding their ranges in response to climate changes or species introductions. Expansion-related selection likely drives the evolution of dispersal and reproductive traits, especially in invasive species introduced into novel habitats. We used an agent-based model to investigate these relationships in the red imported fire ant, *Solenopsis invicta*, by tracking simulated populations over 25 years. Most colonies of this invasive species produce two types of queens practicing alternate reproductive strategies. Claustral queens found new colonies in vacant habitats, while parasitic queens take over existing colonies whose queens have died. We investigated how relative investment in the two queen types affects population demography, habitat occupancy, and range expansion. We found that parasitic queens extend the ecological lifespan of colonies, thereby increasing a population's overall habitat occupancy as well as average colony size (number of workers) and territory size. At the same time, investment in parasitic queens slowed the rate of range expansion by diverting investment from claustral queens. Divergent selection regimes caused edge and interior populations to evolve different levels of reproductive investment, such that interior populations invested heavily in parasitic queens whereas those at the edge invested almost entirely in claustral queens. Our results highlight factors shaping ant life histories, including the evolution of social parasitism, and have implications for the response of species to range shifts.

Keywords

Agent-based Model, Dispersal Evolution, Dispersal Polymorphisms, Invasions, Reproductive Polymorphisms, Range Expansion, Social Parasitism, *Solenopsis invicta*

Introduction

Many species throughout the world are shifting or expanding their ranges in response to climate changes or species introductions (Parmesan et al. 1999, Hickling et al. 2006, Chen et al. 2011). Range shifts may in turn drive evolutionary changes, as populations colonize vacant habitats and experience novel conditions (Thomas et al. 2001, Sexton et al. 2009). Populations at expanding range edges, in particular, are likely to evolve greater dispersal ability as a result of both selection and assortative mating (Cwynar and MacDonald 1987, Phillips et al. 2008, Hill et al. 2011). Other traits that are linked to dispersal, such as fecundity or mating system, may also evolve in response to range expansion (Burton et al. 2010, Hargreaves and Eckert 2014).

Ants present some of the world's most conspicuous recent range expansions. Many species are global invasives whose non-native ranges are expanding through natural and human-assisted dispersal (Holway et al. 2002). Colonies of most ant species reproduce and disperse by rearing winged queens that fly to locate mates and new nest sites (Hölldobler and Wilson 1990, Peeters and Ito 2001). There are countless variants of this life cycle (Heinze and Tsuji 1995, Heinze 2008), and many ants pursue multiple reproductive strategies (Ross and Keller 1995, Sundström 1995, Heinze and Keller 2000). In some species, for example, colonies can produce two different types of queens from the same genome—an independent one that founds new colonies and a parasitic one that joins existing colonies of the same species (Bourke and Franks 1991, Rüppell and Heinze 1999). These alternate strategies result in dispersal differences, since only one queen type can colonize vacant sites while the other can reproduce only in occupied areas. Reproductive polymorphisms have been documented in many invasive ants (Yamauchi and Ogata 1995, Holway et al. 2002, Tsutsui and Suarez 2003), and trait variability has been linked to invasion success in several other taxa (Richards et al. 2006, Davidson et al. 2011, Forsman 2014, González-Suárez et al. 2015). But it remains unclear how reproduction-dispersal polymorphisms in ants affect rates of range expansion, or how investment in different strategies responds to expansion-related selection.

The red imported fire ant (*Solenopsis invicta*), perhaps the best-known invasive ant, is an ideal organism for examining these relationships. It is native to South America but was accidentally introduced to the southeastern USA in the 1930s and to several other countries afterward (Tschinkel 2013). It has been expanding its non-native ranges ever since through human transport and natural dispersal during mating flights (Tschinkel 2013). Most populations of *S. invicta* are monogyne, with a single reproductive queen per colony (Porter et al. 1997). Mature monogyne colonies reproduce using both claustral and parasitic queens (Tschinkel 1996, DeHeer and Tschinkel 1998). Claustral queens fly in spring and summer and found new colonies independently. They dig nest cavities in unoccupied soil, lay eggs, and rear a first generation of workers from their own energy reserves. The parasitic queens, in contrast, fly in late winter and take over conspecific colonies whose queens have recently died, thereby inheriting an existing workforce. Parasitic queens make up a minority of a colony's reproductive

effort (Morrill 1974), but are thought to provide a substantial return per investment due to the constant natural orphaning of colonies in mature populations (DeHeer and Tschinkel 1998).

Using *S. invicta* as a model, this study addresses two questions related to range expansion and alternative reproductive strategies. The first question, posed from the perspective of a population ecologist, asks how investment in parasitic queens affects the spatial distributions of fire ant populations with regard to colony size (number of workers in a colony), territory size (area controlled by a colony), and the propensity to expand into suitable habitats. The second question takes an evolutionary perspective and asks what the optimal relative investment in the two strategies is for colonies seeking to maximize their contribution to future generations.

The presence of parasitic queens in a population makes colonies potentially immortal. Genetic lineages within a colony are replaced over time as queens die and new ones take over. But the colony itself may remain on the landscape for generations, as long as it is successfully parasitized every time it is orphaned. This scenario prompted us to conceive the *Immortality Hypothesis*, which entails three predictions associated with extending the ecological lifespan of colonies. First, parasitic queens should increase the average colony size in a landscape. Second, parasitic queens should increase occupancy of the habitat by fire ant colonies (Korzukhin and Porter 1994). Third, in expanding ranges, investment in parasitic queens should slow range expansion by diverting investment from claustral queens that colonize vacant sites. Alternatively, investment in parasitic queens may speed up range expansion by increasing the average size and persistence of colonies, thereby increasing overall queen production.

From the perspective of a reproductive queen, the optimal investment in daughters practicing the two strategies probably varies with location. Colonies at an expanding edge should experience more reproductive success by investing heavily in claustral daughters that can colonize empty habitat. On the other hand, colonies in the saturated range interior should benefit more from investment in parasitic daughters, as empty habitat is scarce and there are plenty of established colonies with recently deceased queens. Under what we call the *Optimal Investment Hypothesis*, relative investment in claustral versus parasitic queens should evolve as populations expand. In particular, the average investment in claustral queens should increase from the core to the range edge.

We evaluate these hypotheses using an agent-based computer model to track dispersal and colony founding in expanding fire ant populations over 25 years. To examine the ecological effects of reproduction-dispersal polymorphisms, we compare demography, habitat occupancy, and range expansion among populations differing in relative investment in claustral versus parasitic queens. To examine fitness implications of the two strategies, we monitor changes in relative investment within a single variable population as it expands. While we focus on the dynamics of range shifts, our results also provide insight into factors shaping the evolution of reproductive strategies in ants.

Methods

Model design

We constructed an agent-based model in the program R (R Core Team 2012), which simulated the behavior of individual queens and colonies, and allowed us to examine properties of populations of interacting individuals. The inputs to our model determined colony growth and death, competitive territory growth, reproduction and dispersal through the production of new queens, and the relative amount of biomass invested in the production of claustral versus parasitic queens. With these first principles in place, we seeded hypothetical arenas with colonies possessing specified combinations of traits. The arenas were 50 meters wide and bounded on three sides, but unlimited on the upward edge, allowing populations to expand indefinitely. After seeding the arenas with starting populations of colonies, we then monitored how the populations behaved over time (Figure 1). Appendix A provides a detailed description of the model, and the R code can be accessed at the following Github repository: https://github.com/Eli-S-Bridge/RIFA_ABM.

Experimental design

We ran two sets of simulations, the first to examine the effects of reproductive polymorphisms on populations, and the second to examine the fitness implications for colonies investing in the two reproductive strategies. For the first set of simulations, we seeded arenas with 50 colonies that all invested the same amount of effort in claustral versus parasitic queens. We then ran each simulation for 300 months (25 years). Each simulation represented one of six treatments, wherein the proportion of effort that colonies invested in claustral queens was set to 1, 0.98, 0.95, 0.90, 0.75, or 0.50. We ran 72 simulations for each treatment using a C4.8xlarge virtual computer available through Amazon Web Services, which allowed us to run 36 simulations at a time. After accounting for failed simulations (see Appendix A), we ended up with 67 to 69 replicates of each treatment for a total of 407 simulations ($n = 69$ at relative claustral investment = 1; $n = 68$ at 0.98, 0.95, and 0.90; and $n = 67$ at 0.75 and 0.5). We then compared demography, habitat occupancy, and range expansion among the populations that emerged from the six treatments after 300 months.

For each simulation in this first set, we measured the average colony size, average territory size, percentage of available area occupied by all colonies, percentage of colonies headed by parasitic queens, and the maximum upward extent of the range. The upward extent was defined by the maximum y-coordinate among all the territory outlines. To examine spatial patterns we divided the occupied area into sampling windows that were 5 meters high in the up-down axis and extended across the 50-meter width of the arena. We focused on colony size rather than age, because in fire ants (and other social insects) a colony's size is a better indicator of its ecological impact and reproductive potential. Moreover, a colony's size at any age can vary over orders of magnitude due to environmental factors and competitive interactions (Tschinkel 2013).
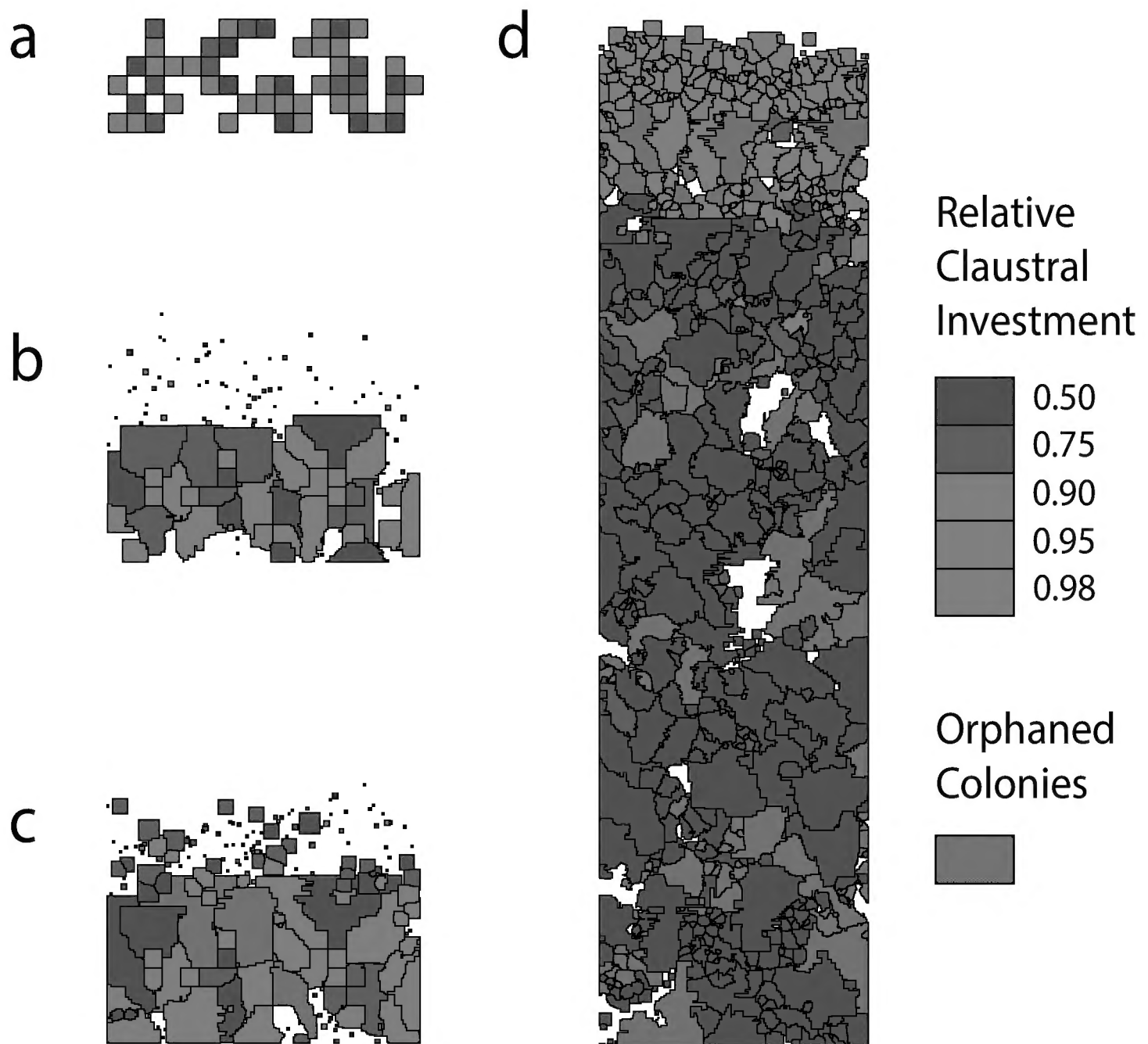
Figure 1. Example simulation of a mixed population consisting of several lineages. **a** Simulation after 0 months, showing starting conditions **b** after 22 months, after the first season of dispersal **c** after 34 months, showing orphaned colonies (gray); and **d** 300 months, at the end of the simulation. Simulation arenas are 50 meters wide. Colors represent lineages that invest different amounts of effort in claustral versus parasitic queens.

The second set of simulations investigated fitness and optimal investment of colonies producing the two queen types. For these simulations, we seeded each arena with 50 colonies varying in relative claustral investment. Each of five levels of investment—0.98, 0.95, 0.90, 0.75, and 0.5—was represented by 10 starting colonies, yielding an initial average claustral investment of 0.847. We then ran the simulation for 300 months (25 years), allowing average claustral investment to evolve through the differential survival and reproduction of colonies with different levels of claustral investment (Figure 1d). We ran 72 simulations using the virtual computer described above, resulting in 66 completed replicates. At the end of the simulation we measured the average claustral investment among colonies large enough to reproduce (≥30,000 workers, Appendix A) in 5 × 50 meter sampling windows.

Results

Population effects

Simulated colony size and territory distributions matched those observed in the field, such that populations consisted of many small colonies and few large ones (Tschinkel 2013), with territories closely packed and irregularly shaped (Adams 1998, Figure 1). As predicted by the Immortality Hypothesis, investing in parasitic queens increased average colony size by 23 to 92% over populations producing only claustral queens (ANOVA $F_{5, 401}$ = 723.4, P = 2 × 10^{-16}, Figure 2a). Every decrease in claustral investment below 0.98 increased average colony size in the population (Tukey's post-hoc tests, 1 to 0.98 comparison P = 0.997; all other Ps < 10^{-7}), from a low of 9,306 workers per colony at total claustral investment to 17,877 workers per colony at half claustral investment. The same results occur when comparing colony territory sizes (ANOVA $F_{5, 401}$ = 850.5, P = 2 × 10^{-16}, Figure 2b). Mean territory size in the population increased by up to 133% over populations producing only claustral queens. Every increase in parasitic investment increased average territory size (Tukey's post-hoc tests, all Ps < 10^{-7}), from a low of 7.2 m^2 at total claustral investment to 16.8 m^2 at half investment. Even a 2% decrease in claustral investment, from 1 to 0.98, caused a 15% increase in average territory size to 8.26 m^2.

Also as predicted, fire ant colonies occupied up to 12% more of the available habitat in populations that produced parasitic queens (Figure 3a). In all populations habitat occupancy fluctuated around consistently high values before dropping to zero at the expanding range margin. But fluctuations were dampened and habitat occupancy was usually higher in populations producing parasitic queens. Mean habitat occupancy over the whole range varied from 75.3% (±2.57) in populations that produced only claustral queens to 84.5% (±2.68) in those that invested half their effort in parasitic queens. These values correspond well with rough field estimates of fire ant territory coverage of available habitat (>90%, Korzukhin and Porter 1994).

The observed changes in demography and habitat occupancy were driven by the parasitic takeover of orphaned colonies. Even a slight increase in the production of parasites, from 0 to 2% of reproductive investment, led to an average of 43.1% (±20.2%) of colonies being headed by parasitic queens (Figure 3b). In populations investing a fourth to a half of their effort in parasites, there were regions where nearly 100% of colonies were headed by parasitic queens (range-wide average of 75.4 ±31.6% for 0.75 claustral investment, 74.8 ±33.7% for 0.5 claustral investment).

Despite its positive effects on average colony size and persistence, investment in parasitic queens decreased the rate of range expansion by up to 4% (ANOVA $F_{5, 401}$ = 43.593, P = 2 × 10^{-16}, Figure 4), from an average maximum of 196.2 (±3.1) meters per simulation in totally claustral populations to 188.8 (±3.2) meters in populations investing half their effort in parasitic queens. Decreasing investment in claustral queens from 1 to 0.9 had no effect (Tukey's post-hoc tests, P > 0.137), but further decreases
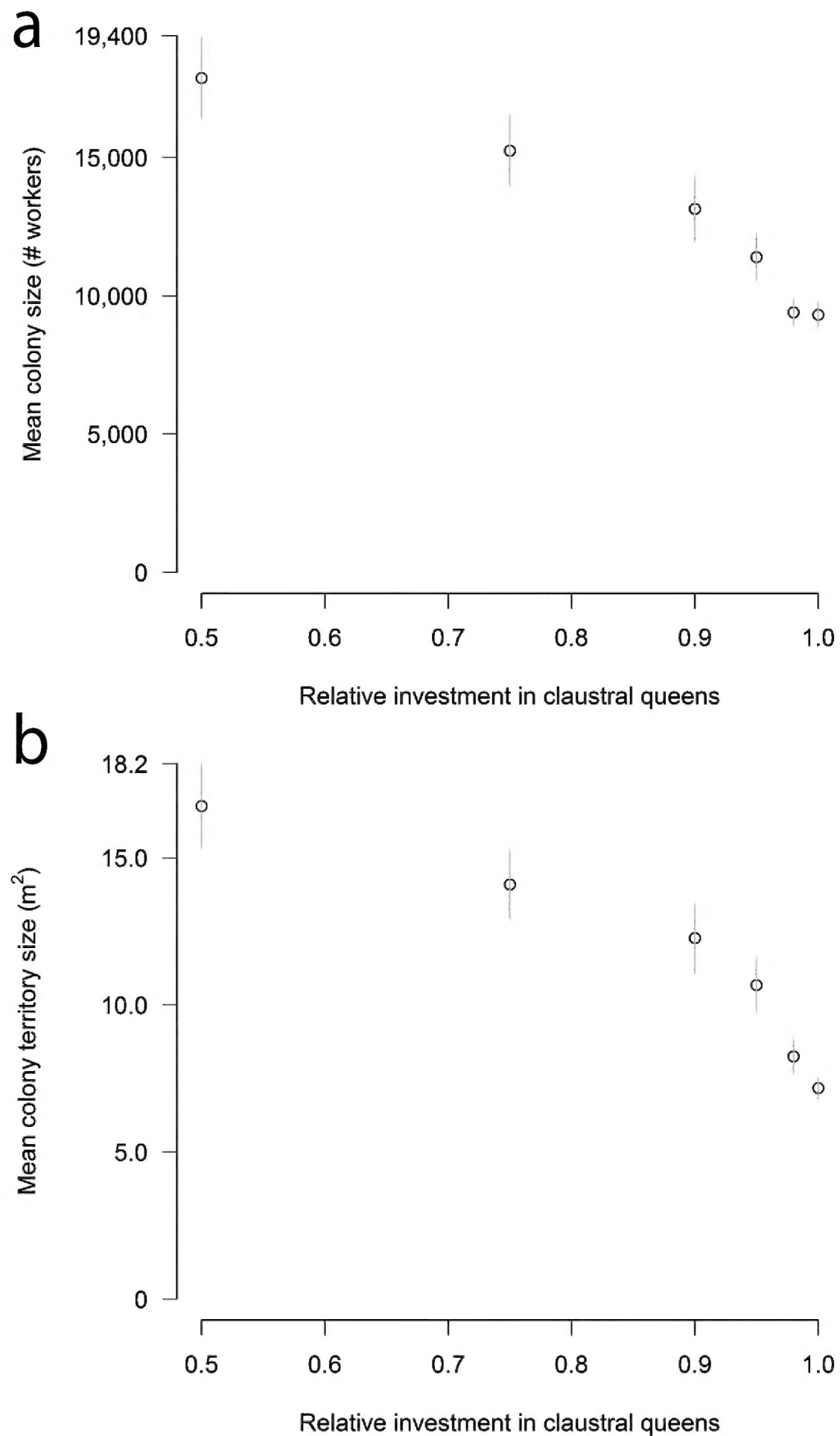
Figure 2. Colony and territory sizes versus reproductive investment. Because parasitic queens extend the ecological lifespan of colonies, populations that invest more in parasitic queens experience larger average colony sizes (**a**) and colony territory areas (**b**). Points show means over all simulations for a given reproductive investment, and error bars show standard deviations. In (a), all values differ ($P < 0.001$) except for those at 1 and 0.98 relative investment ($P = 0.997$); in **b** all values differ ($P < 0.001$).
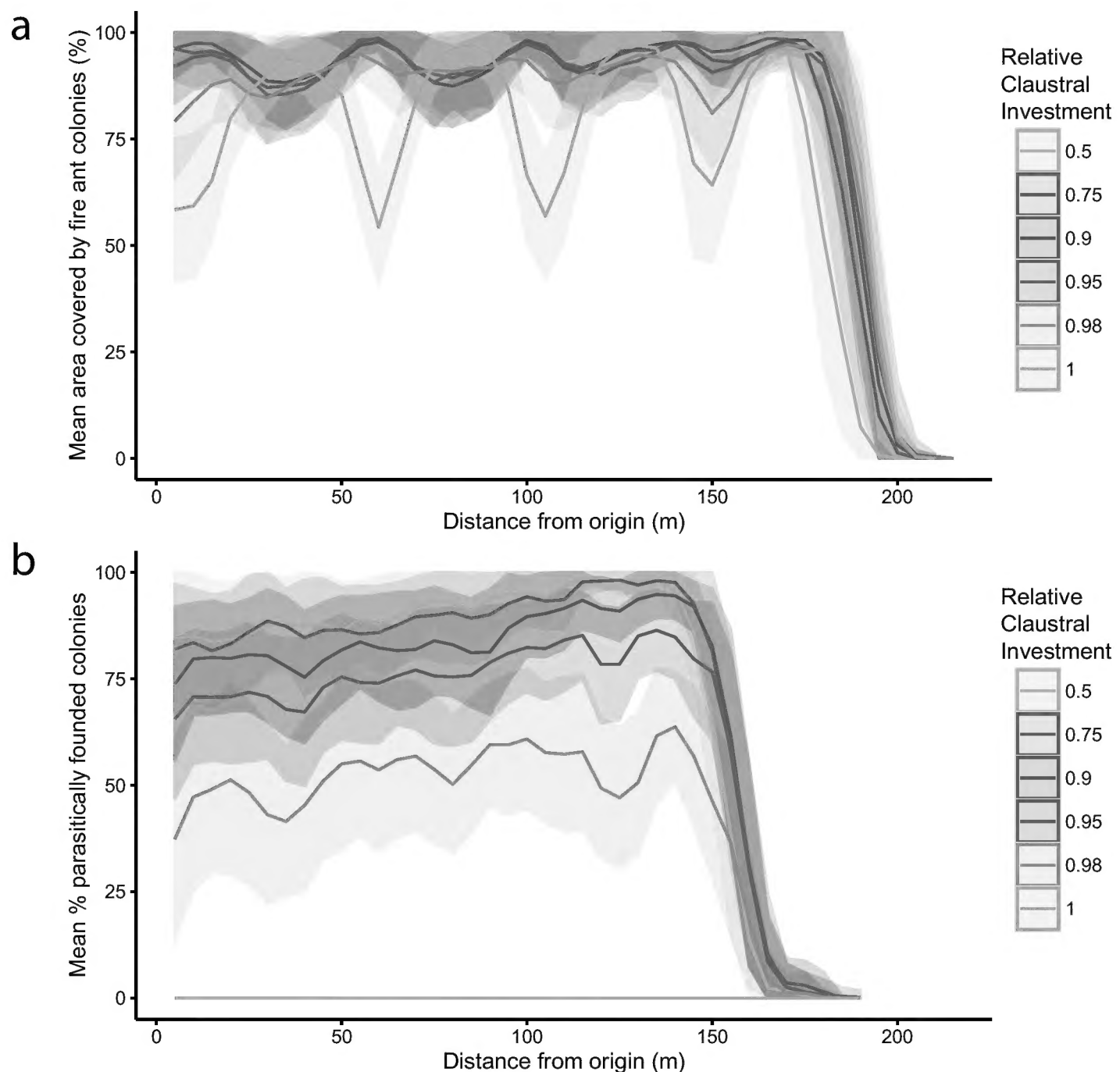
Figure 3. a Percentage of available habitat occupied by fire ant colonies versus distance from the origin (bottom) of a range. Investment in parasitic queens increases and stabilizes the amount of habitat occupied by fire ant colonies **b** The percentage of all colonies that are headed by a parasitic queen versus distance from the origin of a range. Even small investments in parasitic queens lead to high proportions of parasitically founded colonies in the range interior. In all simulations, only claustrally founded colonies occur at the extreme range edge. Colors denote different levels of reproductive investment, lines show averages over all simulations for a given investment, and shading shows standard deviations.

to 0.75 or 0.5 slowed range expansion ($P < 0.003$). Parasites thus appear to affect range expansion primarily by slowing it down through the diversion of investment from claustral queens that can colonize vacant sites, rather than speeding it up by stabilizing larger, more productive colonies.
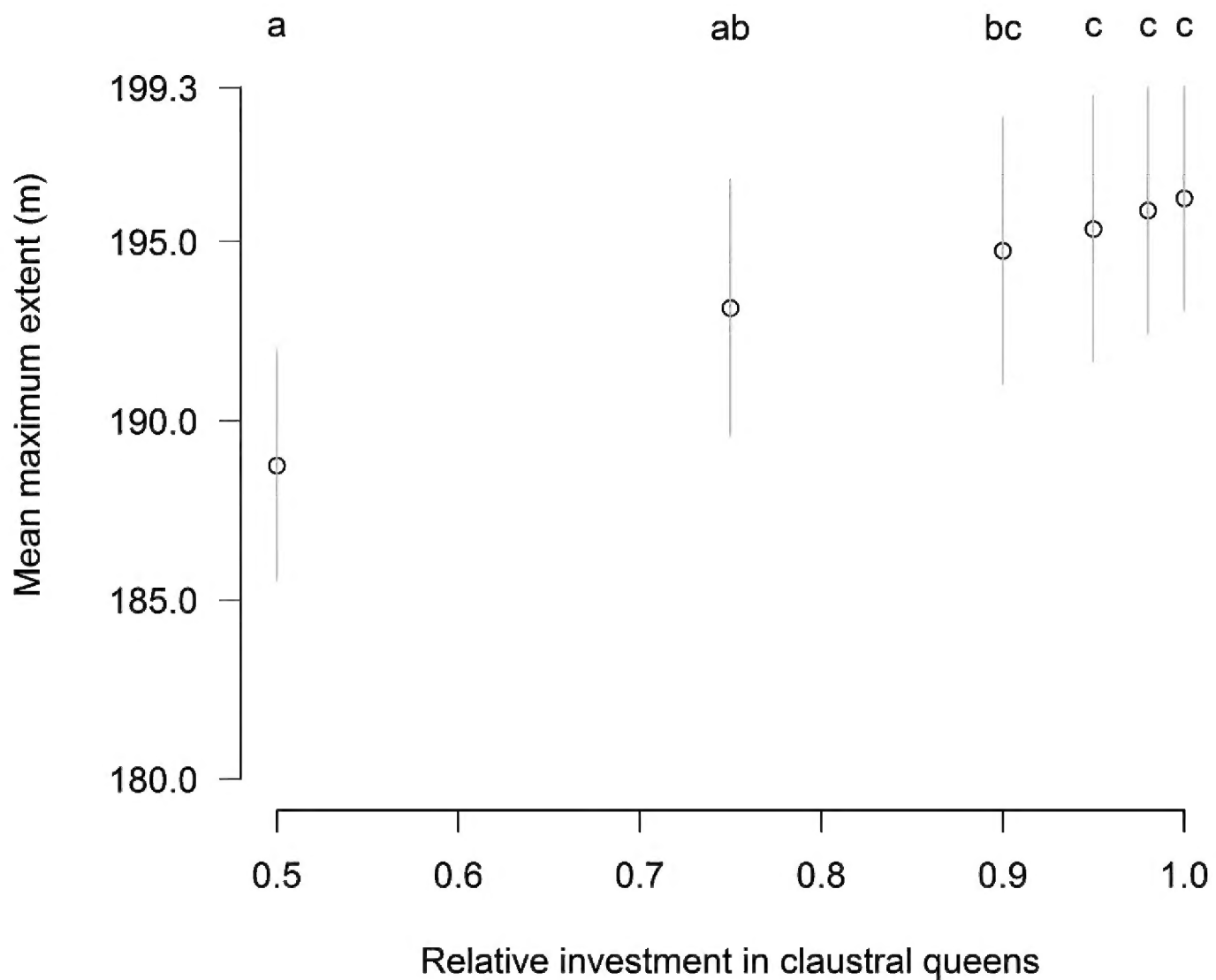
Figure 4. Range expansion versus reproductive investment. Investment in parasitic queens slows range expansion by diverting resources from the production of claustral queens. Points show mean maximum extents of spreading populations over all simulations for a given reproductive investment, and error bars show standard deviations. Points with different letters differ at $P < 0.003$.

Optimal investment

Mature colonies occurred at an average density of 323 ±119 colonies per hectare ($n =$ 66), which is strikingly similar to field estimates from monogyne populations in the southern USA (300 ±240 colonies/ha, Porter et al. 1991). Core and edge populations experienced divergent selection regimes during range expansion. As predicted by the Optimal Investment Hypothesis, a pattern emerged over the course of every simulation wherein colonies in the range interior invested more heavily in parasitic queens and less in claustral queens (Figure 5). The innermost populations averaged slightly above 50% investment in claustral queens (minimum 0.51 ±0.028), which was the minimum allowed in our simulation. At the same time, edge populations retained a heavy investment in claustral queens, with average values approaching 100% (maximum claustral investment 0.96 ±0.015). In these simulations, expansion-related selection has created a geographic gradient in life history strategy within a single variable species.
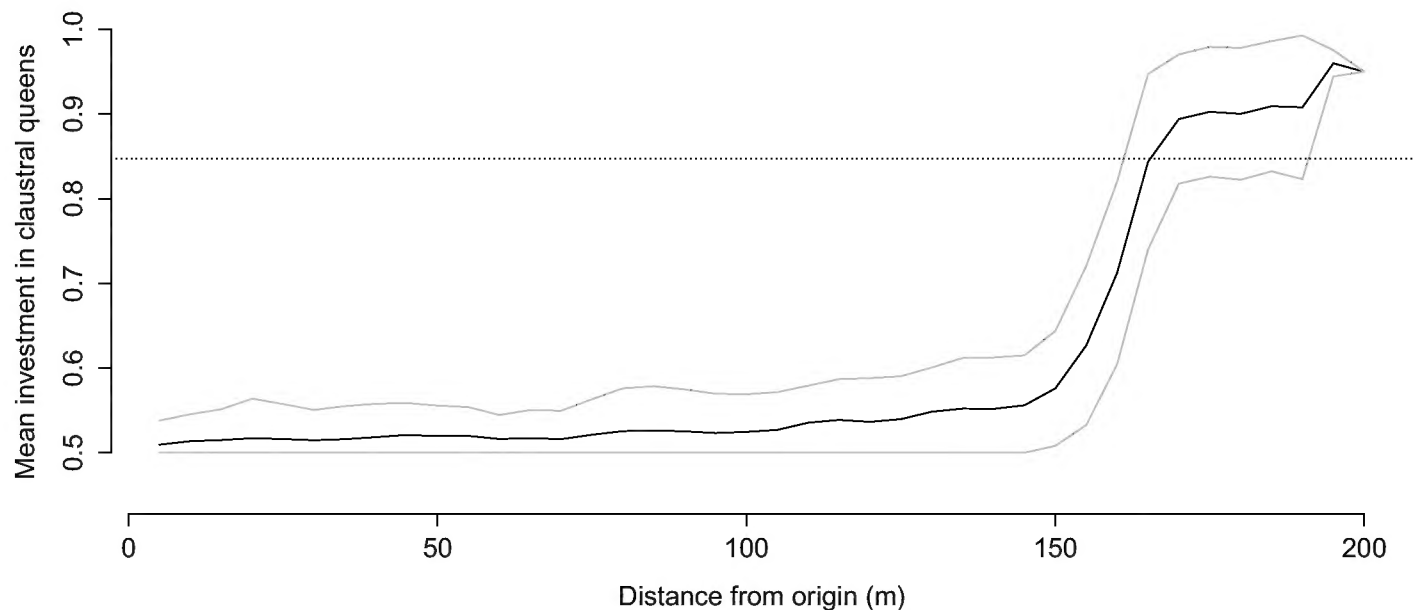
Figure 5. Mean reproductive investment of mature colonies from the range origin (bottom) to the top edge. Gray lines show standard deviations, dashed line shows starting average of 0.847. Populations in the saturated range interior evolve greater investment in parasitic queens, while those at the uninhabited range edge retain greater investment in dispersing claustral queens.

Discussion

Range expansion is a defining character of invasive ants. In species practicing alternate life histories, range dynamics are likely affected by relative investment in different strategies. In our simulations of red imported fire ants, the production of parasitic queens resulted in larger average colony and territory sizes and higher habitat occupancy. On the other hand, by diverting investment from claustral queens that can colonize vacant habitats, the production of parasitic queens slowed range expansion. Range expansion in turn affected the fitness of colonies producing the two queen types. Colonies at expanding range edges benefitted more by investing in claustral queens that could colonize the surrounding vacant habitat, whereas those in the crowded range interior profited from investing more in parasitic queens that could take over orphaned colonies. Divergent selection regimes appeared to drive the evolution of different levels of reproductive investment based on their distance from the range edge.

The effects of range expansion also shed light on other factors shaping the evolution of reproductive strategies in ants. Parasitic founding is thought to be more beneficial in stable saturated environments, and claustral founding to be more beneficial in vacant or disturbed habitats (DeHeer and Tschinkel 1998, Tschinkel 2013). The evolved population differences in our simulations support this notion and also parallel differences among co-occurring fire ant species in the field. Along the US Gulf Coast, *Solenopsis invicta* lives alongside the closely related tropical fire ant, *Solenopsis geminata*, which has a similar life cycle (McInnes and Tschinkel 1995). Within this range, the introduced *S. invicta* occurs primarily in highly disturbed anthropogenic habitats, while the native *S. geminata* occupies more stable natural habitats (Tschinkel 1988b). These habitat differences are mirrored by reproductive differences, with *S.*

geminata investing three to four times as much effort in parasitic queens than *S. invicta* (33% of investment versus <10%). Similarly, our results suggest that within a species older populations should evolve a more parasitic, less dispersive, lifestyle than recently established ones.

Our simulated populations generally behaved realistically, highlighting the model's value for investigating fire ant ecology. Our populations displayed near total occupancy of available habitat (Korzukhin and Porter 1994), closely packed irregularly shaped territories (Adams 1998), size distributions consisting of many small colonies and a few large ones (Tschinkel 2013), and population densities similar to those in the field (323 ±119 colonies/ha simulated versus 300 ±240 in the field, Porter et al. 1991). We note, on the other hand, that in our simulated populations, the observed frequency of parasitic founding and the optimal reproductive investment in interior colonies (>40% of colonies headed by parasites, 40–50% investment in parasitic queens) more accurately describe the native *S. geminata* (35% of colonies, 33% investment in parasites, McInnes and Tschinkel 1995) than *S. invicta* (3.5% of colonies, <10% investment in parasites, DeHeer and Tschinkel 1998). Our goal is not to make absolute predictions about fire ant biology, however, but rather to investigate the interplay between reproductive strategy and range dynamics within a given species.

We made several simplifying assumptions in constructing our model. We assumed, for example, that habitat is constant and homogeneous and that lineages do not interbreed. Incorporating disturbance—to better capture the ecological preferences of *S. invicta*—would shift optimal investment toward more claustral queens by providing a steady supply of vacant habitat in which to found colonies. Allowing gene flow among lineages would slow divergence between interior and edge populations, probably shifting investment toward more claustral queens in the interior. Programing farther dispersal distances (see Appendix A) would probably make the transition between interior and edge populations more gradual, and allowing claustral investment to drop below 50% may reveal upper limits to parasitic investment or shed light on the evolution of obligate parasitism. Furthermore, a substantial minority of fire ant populations in the field (≤20%, Porter et al. 1997) are polygyne and practice fundamentally different life histories in which colonies contain many unrelated queens and reproduce vegetatively by budding or splitting (Tschinkel 2013). Finally, introduced populations of *S. invicta* compete with (Porter et al. 1988, Tschinkel 1988b) or hybridize with (Ometto et al. 2012) other fire ant species, creating a complex network of interspecific interactions affecting dispersal, colony growth, and reproductive success. A complete model of fire ant invasions would incorporate all these variants, and is beyond the scope of our current study.

The rapid spread of several invasive ant species around the globe, through multiple introduction events, provides a valuable opportunity to investigate the interplay between range expansion, dispersal, and reproduction. Because small differences in reproductive strategy cause pervasive changes in demography, habitat occupancy, range expansion, and the response to expansion-related selection, founder effects may play a major role in determining the ecological impacts of introduced ants. Subsequent

selection associated with rapid range expansion may further shape the evolution of introduced populations. For similar reasons, some native ant species may be unable to shift their ranges rapidly enough to track climatic changes, and those that do may experience changes in dispersal ability or reproductive ecology as a result. In a world where ant range shifts are increasingly likely (Colwell et al. 2008), predicting these outcomes has substantial practical importance. Agent-based models are a useful approach for addressing these issues, given sufficiently detailed life history inputs, and provide a relatively rapid and low-cost method of examining future scenarios.

Acknowledgements

References

Adams ES (1998) Territory size and shape in fire ants: a model based on neighborhood interactions. Ecology 79: 1125–1134. https://doi.org/10.1890/0012-9658(1998)079[1125:TSASIF]2.0.CO;2

Bivand RS, Pebesma EJ, Gomez-Rubio V (2013) Applied spatial data analysis with R, Second edition. Springer, New York. https://doi.org/10.1007/978-1-4614-7618-4

Bivand R, Rundel C (2015) rgeos: Interface to Geometry Engine – Open Source (GEOS). R package version 0.3-12. http://CRAN.R-projectorg/package=rgeos

Blondel E (2015) cleangeo: Cleaning Geometries from Spatial Objects. R package version 0.1-1. http://CRAN.R-project.org/package=cleangeo

Booth K, Dhami M (2008) Red Imported Fire Ant (*Solenopsis invicta*): A review of the literature regarding the determination of colony age. A report prepared for MAF Biosecurity in New Zealand. Centre for Biodiversity and Biosecurity, University of Auckland.

Bourke AFG, Franks NR (1991) Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. Biological Journal of the Linnean Society 43: 157–178. https://doi.org/10.1111/j.1095-8312.1991.tb00591.x

Burton OJ, Phillips BL, Travis JMJ (2010) Trade-offs and the evolution of life-histories during range expansion. Ecology Letters 13: 1210–1220. https://doi.org/10.1111/j.1461-0248.2010.01505.x

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333: 1024–1026. https://doi.org/10.1126/science.1206432

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT (2008) Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. Science 322: 258–261. https://doi.org/10.1126/science.1162547

Cwynar LC, MacDonald GM (1987) Geographical variation of lodgepole pine in relation to population history. The American Naturalist 129: 463–469. https://doi.org/10.1086/284651

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14: 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

DeHeer CJ, Tschinkel WR (1998) The success of alternative reproductive tactics in monogyne populations of the ant *Solenopsis invicta*: significance for transitions in social organization. Behavioral Ecology 9: 130–135. https://doi.org/10.1093/beheco/9.2.130

Forsman A (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. Proceedings of the National Academy of Sciences of the United States of America 111: 302–307. https://doi.org/10.1073/pnas.1317745111

González-Suárez M, Bacher S, Jeschke JM (2015) Intraspecific Trait Variation is Correlated with Establishment Success of Alien Mammals. The American Naturalist 185: 737–746. https://doi.org/10.1086/681105

Hargreaves AL, Eckert CG (2014) Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. Functional Ecology 28: 5–21. https://doi.org/10.1111/1365-2435.12170

Heinze J (2008) The demise of the standard ant (Hymenoptera: Formicidae). Myrmecological News 11: 9–20.

Heinze J, Keller L (2000) Alternative reproductive strategies: a queen perspective in ants. Trends in Ecology & Evolution 15: 508–512. https://doi.org/10.1016/S0169-5347(00)01995-9

Heinze J, Tsuji K (1995) Ant Reproductive Strategies. Researches on Population Ecology 37: 135–149. https://doi.org/10.1007/BF02515814

Helms JA, IV, Godfrey A (2016) Dispersal Polymorphisms in Invasive Fire Ants. PLoS ONE 11: e0153955. https://doi.org/10.1371/journal.pone.0153955

Helms JA, IV, Godfrey A, Ames T, Bridge ES (2016a) Are invasive fire ants kept in check by native aerial insectivores? Biology Letters 12. https://doi.org/10.1098/rsbl.2016.0059

Helms JA, IV, Godfrey A, Ames T, Bridge ES (2016b) Predator foraging altitudes reveal the structure of aerial insect communities. Scientific Reports 6: 28670. https://doi.org/10.1038/srep28670

Helms JA, Kaspari M (2014) Found or Fly: Nutrient loading of dispersing ant queens decreases metrics of flight ability (Hymenoptera: Formicidae). Myrmecological News 19: 85–91.

Helms JA, IV, Kaspari M (2015) Reproduction-dispersal tradeoffs in ant queens. Insectes Sociaux 62: 171–181. https://doi.org/10.1007/s00040-015-0391-9

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12: 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hill JK, Griffiths HM, Thomas CD (2011) Climate Change and Evolutionary Adaptations at Species' Range Margins. Annual Review of Entomology 56: 143–159. https://doi.org/10.1146/annurev-ento-120709-144746

Hölldobler B, Wilson EO (1990) The Ants. Belknap Press of Harvard University Press, Cambridge. https://doi.org/10.1007/978-3-662-10306-7

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The Causes and Consequences of Ant Invasions. Annual Review of Ecology and Systematics 33: 181–233. https://doi.org/10.1146/annurev.ecolsys.33.010802.150444

Korzukhin MD, Porter SD (1994) Spatial Model of Territorial Competition and Population Dynamics in the Fire Ant *Solenopsis invicta* (Hymenoptera: Formicidae). Environmental Entomology 23: 912–922. https://doi.org/10.1093/ee/23.4.912

Markin GP, Dillier JH, Collins HL (1973) Growth and Development of Colonies of the Red Imported Fire Ant, *Solenopsis invicta*. Annals of the Entomological Society of America 66: 803–808. https://doi.org/10.1093/aesa/66.4.803

McInnes DA, Tschinkel WR (1995) Queen dimorphism and reproductive strategies in the fire ant *Solenopsis geminata* (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology 36: 367–375. https://doi.org/10.1007/BF00177332

Morrill WL (1974) Production and Flight of Alate Red Imported Fire Ants. Environmental Entomology 3: 265–271. https://doi.org/10.1093/ee/3.2.265

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (2001) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583. https://doi.org/10.1038/21181

Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. R News 5: 9–13.

Peeters C, Ito F (2001) Colony Dispersal and the Evolution of Queen Morphology in Social Hymenoptera. Annual Review of Entomology 46: 601–630. https://doi.org/10.1146/annurev.ento.46.1.601

Phillips BL, Brown GP, Travis JMJ, Shine R (2008) Reid's Paradox Revisited: The Evolution of Dispersal Kernels during Range Expansion. The American Naturalist 172: S34–S48. https://doi.org/10.1086/588255

Porter SD, Bhatkar A, Mulder R, Vinson SB, Clair DJ (1991) Distribution and Density of Polygyne Fire Ants (Hymenoptera: Formicidae) in Texas. Journal of Economic Entomology 84: 866–874. https://doi.org/10.1093/jee/84.3.866

Porter SD, Tschinkel WR (1986) Adaptive Value of Nanitic Workers in Newly Founded Red Imported Fire Ant Colonies (Hymenoptera: Formicidae). Annals of the Entomological Society of America 79: 723–726. https://doi.org/10.1093/aesa/79.4.723

Porter SD, Van Eimeren B, Gilbert LE (1988) Invasion of Red Imported Fire Ants (Hymenoptera: Formicidae): Microgeography of Competitive Replacement. Annals of the Entomological Society of America 81: 913–918. https://doi.org/10.1093/aesa/81.6.913

Porter SD, Williams DF, Patterson RS, Fowler HG (1997) Intercontinental Differences in the Abundance of *Solenopsis* Fire Ants (Hymenoptera: Formicidae): Escape from Natural Enemies? Environmental Entomology 26: 373–384. https://doi.org/10.1093/ee/26.2.373

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, ISBN 3–900051–07–0. http://www.R-project.org

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Ross KG, Keller L (1995) Ecology and Evolution of Social Organization: Insights from Fire Ants and Other Highly Eusocial Insects. Annual Review of Ecology and Systematics 26: 631–656. https://doi.org/10.1146/annurev.es.26.110195.003215

Rüppell O, Heinze J (1999) Alternative reproductive tactics in females: the case of size polymorphism in winged ant queens. Insectes Sociaux 46: 6–17. https://doi.org/10.1007/s000400050106

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and Ecology of Species Range Limits. Annual Review of Ecology, Evolution, and Systematics 40: 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sundström L (1995) Dispersal polymorphism and physiological condition of males and females in the ant, *Formica truncorum*. Behavioral Ecology 6: 132–139. https://doi.org/10.1093/beheco/6.2.132

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. Nature 411: 577–581. https://doi.org/10.1038/35079066

Tschinkel WR (1987) Fire Ant Queen Longevity and Age: Estimation by Sperm Depletion. Annals of the Entomological Society of America 80: 263–266. https://doi.org/10.1093/aesa/80.2.263

Tschinkel WR (1988a) Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. Behavioral Ecology and Sociobiology 22: 103–115. https://doi.org/10.1007/BF00303545

Tschinkel WR (1988b) Distribution of the Fire Ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in Northern Florida in Relation to Habitat and Disturbance. Annals of the Entomological Society of America 81: 76–81. https://doi.org/10.1093/aesa/81.1.76

Tschinkel WR (1992) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. Ecological Entomology 17: 179–188. https://doi.org/10.1111/j.1365-2311.1992.tb01176.x

Tschinkel WR (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecological Monographs 63: 425–457. https://doi.org/10.2307/2937154

Tschinkel WR (1996) A newly-discovered mode of colony founding among fire ants. Insectes Sociaux 43: 267–276. https://doi.org/10.1007/BF01242928

Tschinkel WR (2013) The Fire Ants. Belknap Press of Harvard University Press, Cambridge.

Tschinkel WR, Adams ES, Macom T (1995) Territory area and colony size in the fire ant *Solenopsis invicta*. Journal of Animal Ecology 64: 473–480. https://doi.org/10.2307/5650

Tsutsui ND, Suarez AV (2003) The Colony Structure and Population Biology of Invasive Ants. Conservation Biology 17: 48–58. https://doi.org/10.1046/j.1523-1739.2003.02018.x

Vargo EL (1988) Effect of pleometrosis and colony size on the production of sexuals in monogyne colonies of the fire ant *Solenopsis invicta*. In: Trager JC (Ed.) Advances in Myrmecology. E. J. Brill, New York.

Whitcomb WH, Bhatkar A, Nickerson JC (1973) Predators of *Solenopsis invicta* Queens Prior to Successful Colony Establishment. Environmental Entomology 2: 1101–1103. https://doi.org/10.1093/ee/2.6.1101

Yamauchi K, Ogata K (1995) Social Structure and Reproductive Systems of Tramp Versus Endemic Ants (Hymenoptera: Formicidae) of the Ryukyu Islands. Pacific Science 49: 55–68.

Supplementary material 1

Range expansion drives the evolution of alternate reproductive strategies in invasive fire ants

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Data type: species data